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ANNULUS FORMATION ON THE SCALES OF CERTAIN MICHIGAN GAME FISHES *

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THIS investigation on the annulus formation on the scales of Michigan game fishes was begun in September, 1938, when the writer undertook the growth-rate studies for the Institute for Fisheries Research of the Michigan Department of Conservation. It soon became apparent that one of the first problems was to delimit the time or period of year at which the annulus or year mark forms on the scales of certain of the game fishes of Michigan. The precise determination of the age of fish collected in spring and early summer was difficult, and at times impossible, because of the lack of exact information on the time of annulus formation. On many scales it was hard to decide whether the marginal area outside the last annulus represented the new season's increment or the entire last year's growth. If the year mark of the previous winter had already formed, the age as determined by the number of completed annuli would be correct, but if the mark had not been completed, the fish would be one year older than the age indicated by the number of annuli.

In order to solve this main problem conclusively it was necessary to demonstrate that the annulus on the scale of the fishes studied corresponds structurally with the year marks which have been found in various species by other workers, and to secure evidence that the annulus is formed each year and only once annually.

It was apparent, also, that the solution of the problem of the time of annulus formation would contribute in other ways to an understanding of fish growth. For instance, evidence would be secured on the factors responsible for the formation of the annular rings. The periodic sampling would make it possible to determine at which part of the growing season the growth is fastest. It would be possible, also, to trace the course of growth during one season. Furthermore,

* Contribution from the Institute for Fisheries Research of the Michigan Department of Conservation.

an analysis could be made of possible differences in the growth of the sexes, and of various age groups and sizes of fish. Although data were obtained on all these problems, this report is concerned primarily with the time and cause of annulus formation.

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SOURCE OF MATERIALS

For the monthly collection of scale samples which comprise the material used in this investigation eight waters (seven lakes and a pond; Fig. 1) were selected at the beginning of the work. These waters were chosen so as to insure a range of samples for several species from south to north. Collections were made of the species listed at the following places on the dates given:

Clear Lake, Jackson County (area, 137 acres; maximum depth, 35 feet):¹ January, February, April, June, July, and December, 1939, and May and June, 1940. Game species: yellow perch (*Perca flavescens*), largemouth bass (*Huro salmoides*), bluegill (*Lepomis m. macrochirus*), pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites r. rupestris*), and black crappie (*Pomoxis nigro-maculatus*).

Pasinski Pond, Livingston County (area, 4½ acres; maximum depth, 5 feet): September, 1938, April, May, June, July, and September, 1939, and February, 1940. Game species: bluegill.

Budd Lake, Clare County (area, 175 acres; maximum depth, 34 feet): May, June, and October, 1939, and May and June, 1940. Game species: yellow perch, largemouth bass, bluegill, pumpkinseed, rock bass, and black crappie.

Round Lake, Emmet County (area, 336 acres; maximum depth, 27 feet): May, June, and October, 1939, and May and June, 1940. Game species: perch, largemouth bass, bluegill, pumpkinseed, and rock bass.

¹ The descriptive statements regarding each lake are taken from the maps and survey records of the Institute for Fisheries Research.



FIG. 1. Location of the lakes from which the major collections were made and limits of the three temperature zones into which the state was divided

North Manistique Lake, Luce County (area, 1,722 acres; maximum depth, 50 feet): June, July, September, and October, 1939, and May, June, and July, 1940. Game species: yellow perch, walleye (*Stizostedion v. vitreum*), smallmouth bass (*Micropterus d. dolomieu*), and rock bass.

Bass Lake, Marquette County (area, 400 acres; maximum depth, 30 feet): June, July, September, and October, 1939, and May, June, and July, 1940.

Game species: yellow perch, walleye, smallmouth and largemouth bass, bluegill, and pumpkinseed.

Crooked Lake, Gogebic County (area, 566 acres; maximum depth, 66 feet): July, August, September, and October, 1939, and May, June, and July, 1940. Game species: yellow perch, smallmouth and largemouth bass, bluegill, pumpkinseed, and black crappie.

Lake Fannie Hooe, Keweenaw County (area, 231 acres; maximum depth, 48 feet): July, August, September, and October, 1939, and May, June, and July, 1940. Game species: yellow perch, smallmouth bass, bluegill, and rock bass.

In connection with other investigations for the Institute for Fisheries Research some data were taken on three additional lakes:

Standard Lake, Cheboygan, Charlevoix, and Otsego counties (area, 32 acres; maximum depth, 31 feet): May, June, and October, 1939, and May, 1940. Game species: yellow perch, smallmouth bass, and rock bass.

Ford Lake, Otsego County (area, 12 acres; maximum depth, 39 feet): May, 1939, and May, 1940. Game species: bluegill.

Deep Lake, Oakland County (area, 15 acres; maximum depth, 61 feet): February, April, May, June, July, and August, 1939, April, May, June, July, August, and September, 1940, and April, May, June, July, August, and September, 1941. Game species: largemouth bass, bluegill, pumpkinseed, and rock bass.

COLLECTION, PREPARATION, AND EXAMINATION OF SCALE MATERIAL

The collections were made with three to nine gill nets (5 by 125 feet, of five mesh sizes, grading from $1\frac{1}{2}$ to 4 inches, stretched measure), with seines, and with a river fyke net (9 feet long, with 5-foot wings and made with 2-inch stretched-measure mesh). Rod-and-line fishing also was employed in the taking of samples.

Length, weight, sex, and state of sexual maturity were recorded, and scale samples were taken. Both standard length, the length of the fish from the tip of the snout to the end of the vertebral column, and total length, the greatest measurable length of the fish, were recorded to the nearest millimeter. All weights were recorded to the nearest gram, with the exception of those of a few large fish (walleyes), which were weighed to the nearest half ounce.

In the laboratory the scales were prepared in the customary manner and mounted on glass slides in a glycerin-jelly medium. They were examined on a projection machine similar to the one described by Van Oosten, Deason, and Jobes (1934). Measurements were made along the most nearly vertical anterior interradiar space. The positions of the annuli were marked on 1- by 11-inch tagboard strips.

Measurements in millimeters for computations were taken from these strips.

The data were tabulated on "growth-analysis cards" used by the Institute for Fisheries Research, according to species, date of collection, sex and age group, and under age group by size.

THE SCALE METHOD

This investigation is designed to render more precise the determination of the age of fishes by the scale method. The age of the fish is determined by counting the number of annuli or year marks on the scale. The general validity of this method has been assumed. That the annuli on the scales do provide a clue to the fish's age and growth has been demonstrated for many species and is now confirmed for the material used in the present study.

The structure of the scale and the character of the annulus are described below. All the fishes used in the present study have ctenoid scales, which may be exemplified by a photograph (Pl. I, Fig. 1) of a scale from a bluegill, $4\frac{1}{4}$ inches long, caught on June 14, 1939, in Pasinski Pond, Livingston County. In the center of the scale is a very small clear area, the focus, which represents the original scale of the young fish. Around this center are numerous ridges or circuli, which represent successive stages in scale growth, though they seldom correspond exactly with the scale margin. The posterior or free part of the scale bears the ctenii. On the anterior, concealed, field are the radiating grooves, known as radii.

As the scale grows, each circulus is laid down first along the anterior margin and gradually grows around the scale. A close examination usually will show several incomplete circuli along the dorsal and ventral borders of the scale (left and right in the figure). During the winter, growth is retarded or ceases entirely, and the circuli do not grow to completion. With the resumption of rapid growth in the spring a new circulus is laid down which soon grows around the entire scale margin, just outside the incomplete circuli of the previous growing season, which remain as they were in the winter. The new circulus therefore cuts across these incomplete circuli, and this "cutting over" is one of the most conspicuous and trustworthy characteristics of the annulus or year mark.

The cycloid type of scale lacks ctenii. The circuli usually extend around the entire scale, although they may be weak or absent on the

posterior portion. The annulus is formed in the same general manner as on the ctenoid scales, and is recognized by the same criteria. On examination of the scale (Pl. I, Fig. 2) from an 11-inch cisco (*Leucichthys artedii*), caught on December 1, 1934, in Blind Lake, Washtenaw County, it will be seen that there is an alternation of light and dark bands, made up respectively of widely and narrowly spaced circuli. These bands are usually more pronounced on the cycloid scales, although some ctenoid scales exhibit them also, and some scales of either type do not show them.

Early workers treated these distinct zones as summer and winter bands, but failed to define the incomplete circuli as the chief diagnostic character of the annulus. Hoffbauer (1898, 1900), however, had described the true character of the annulus, and had offered proof of its validity as a year mark. Other works of his (1901, 1904, 1905, 1906) provided confirmatory evidence. Masterman (1913) also pointed out the true nature of the annulus on the salmon scale, as Hoffbauer had done for the carp. Nevertheless, many workers (Gilbert, 1922; Snyder, 1923; and others) continued to interpret the "winter band" as the year mark.

The annuli formed on the scales of the game fishes of Michigan that were studied are of the same character as those described by the majority of workers.

Reviews of the literature and bibliographies on the scale method have been given by Thomson (1904), Taylor (1916), Hutton (1921), Creaser (1926), Mohr (1927, 1930, 1934), Graham (1929), and Van Oosten (1929).

The assumption that the annulus is a year mark and that but one annulus forms each year has been and still is under criticism. This question has been studied in a number of experiments. Hoffbauer (1898 to 1906), in presenting the major foundation of the method, followed the growth of carp of known age in a pond for three years, and made observations concerning the scale characteristics of several other species (*Carassius carassius*, *Lucioperca sandra*, *Abramis brama*, *Esox lucius*, *Leuciscus erythrophthalmus*, and *Leuciscus cephalus*). By laboratory or pond experiments Dahl (1911), Mohr (1916), Van Oosten (1923), Creaser (1926), and others furnished basic information on annulus formation. Johnston (1905, 1907) and many later workers, for example, Hutton (1909, 1910), Gilbert (1913), and Fraser (1921), tested the theory by tagging experiments.

Lea (1910), Hjort (1914), and others, in following the dominant year class through commercial catches for several years, determined that one additional annulus appeared on the scales of members of this year class each year. Lea (1911), Fraser (1916, 1917), and others traced the marginal scale growth throughout the year by periodic sampling, and thus obtained evidence to show that only one annulus a year was formed by the species studied.

Contrary evidence also has been gathered which tends to indicate that the determination of the true annuli may not always be a simple matter. Other marks have been described on scales, which, though not true annuli, are often mistaken for them. Jacot (1920) believed that the annulus of the mullet was a migration check. Spawning marks have been described on many scales (Johnston, 1905; Calderwood, 1911, 1914; Hubbs and Cooper, 1935). Hubbs (1921) also described a "metamorphic annulus" on the scales of viviparous perches (Embiotocidae), brought about by a temporary retardation of growth at birth, in the summer. Bennett, Thompson, and Parr (1940) observed that several annuli may form in one season on the scales of a certain percentage of bluegills and largemouth bass in Illinois. Further discussion of this subject will be made in later sections.

FACTORS OF ANNULUS FORMATION

The formation of the annulus is obviously dependent upon the retardation or cessation of growth, followed by a resumption of growth. As Van Oosten (1923) pointed out, growth of the body and scale is closely correlated, and any factor affecting the growth rate of the body may be of primary significance in the formation of the annulus. The problem, then, is largely one of determining the factors that are responsible for the seasonal growth rhythm of the fish.

Temperature

Many authors have held that temperature is the most important factor in the formation of the annulus. The views of Fulton (1904) are as follows: "Temperature is active in modifying the rate of growth by acting directly upon the metabolism of the fish and also by affecting the rapidity of digestion. In very cold water the fishes give up feeding altogether, because the ferments upon which digestion depends do not act, or act very slowly, at low temperatures, and

in fishes, as in other animals, appetite waits on digestion, and this is, on the other hand, correlated with the metabolism in the tissues. It has been shown by Krukenberg that the pepsine or analogous body in the stomach of fish acts as well at 20° C. as at 40° C., at which, among mammals, digestion is most active, and that the rapidity of its action is closely related to the temperature, and Knauthe and Zuntz have shown that the same thing applies to the metabolism in fish, the vital activities being more active in the higher temperature, as shown by the excretion of carbonic acid gas and other products of metabolism."

Thomson (1904) held that "the divergence in growth of the scales during summer and winter is probably due to changes in the general metabolism of the body, which are in their turn, in all probability, the result of seasonal variation in temperature and food supply."

In 1911 Lea stated that there was no close dependence between temperature and growth rate, but that the rate of growth rises as soon as the temperature begins to rise in the spring.

Cutler (1918) wrote in regard to temperature: "The conclusions which I draw from the results of these experiments on the scale growth of fish is, that the broad summer bands, which are caused by the sclerites during the period being wide, and the narrow winter bands, produced by narrow sclerites, are due to changes in the temperature of the water in which the animals live. High temperatures, such as are found in summer months, lead to formation of broad sclerites, while narrow ones are called forth by low winter temperatures."

Van Oosten (1923) stated that "temperature appears to be a primary factor in the formation of annuli in the adults, but only a secondary one in the immature fish."

To determine at just what temperature the annulus forms in southern Michigan a thermograph was set up at Deep Lake, Oakland County, on April 22, 1940. It was removed in September and re-installed on April 18, 1941. The temperature records for the period during which the annulus formed are summarized in Table I.

The data obtained by means of the thermograph indicate that annuli are formed in the spring at a fairly definite temperature. In both 1940 and 1941 no annuli were observed before the mean daily water temperature exceeded 50° F. The mean temperatures of the days on which the collections first showed annulus formation were 53° F. (May 10) in 1940 and 52° F. (April 22) in 1941. The mean

TABLE I

TEMPERATURE RECORD FOR DEEP LAKE DURING PERIOD OF
ANNULUS FORMATION

The thermocouple was located on a shaded area of sandy shoal, on bottom at depth of 18 inches. The dates of annulus formation were May 8-20 in 1940 and April 22-May 5 in 1941.

Week	Temperature, degrees Fahrenheit (Centigrade in parentheses)		
	Mean minimum	Mean	Mean maximum
April 28-May 4, 1940	42 (5.6)	45 (7.2)	49 (9.4)
May 5-11, 1940	49 (9.4)	52 (11.1)	56 (13.3)
May 12-18, 1940	52 (11.1)	55 (12.8)	59 (15.0)
May 19-25, 1940	53 (11.7)	57 (13.9)	60 (15.6)
April 21-27, 1941	48 (8.9)	51 (10.5)	54 (12.2)
April 28-May 4, 1941	56 (13.3)	60 (15.6)	64 (17.8)
May 5-11, 1941	55 (12.8)	59 (15.0)	62 (16.7)
May 12-18, 1941	55 (12.8)	59 (15.0)	62 (16.7)

temperatures of the first days on which a majority of the fish in the collections had formed annuli were 58° F. in both 1940 (May 13) and 1941 (April 28). It should be noticed particularly that the annuli were completed approximately two weeks earlier in 1941 than in 1940, but that the temperatures at the time of annulus formation were almost exactly the same in the two years.

Markus (1932) determined that largemouth bass did not feed readily at 10° C. (50° F.) and that at 4° C. (39° F.) none took food voluntarily. From his experiments Hathaway (1927) reached the following conclusions in regard to bluegill, pumpkinseed, and largemouth bass: "When fishes were tested at 20° [68° F.] and then transferred to 10° the food consumption the first week at 10° was, on the average, about one-third of what it had been at the higher temperature. . . . During the second, third, and fourth weeks at 10° there was, in several cases, a further decline, the average food eaten per day for the fourth week amounting to 27 per cent of what it had been at 20°."

A rough correlation was found between mean monthly air temperatures (drawn from records of the United States Weather Bureau) and the time of annulus formation. This point will be discussed in the section on "Time of Annulus Formation."

Temperatures higher than the optimum for the species also tend to retard or stop growth. Audigè (1921) ascertained that certain temperate-zone fishes (*Cyprinus carpio*, *Carassius auratus*, and *Scardinius erythrophthalmus*) grew irregularly, with frequent checks, when held in water at 24–25° C. (75–77° F.) and that these checks were more pronounced at temperatures between 30° (86° F.) and 31° C. (87.8° F.). Similarly, it is known that the scales of tropical marine fishes often show annulus-like marks far too numerous to represent years. It is possible that the several annulus-like marks which formed in one year on the scales of some of the bluegills and large-mouth bass in Fork Lake, Illinois (Bennett, Thompson, and Parr, 1940), were induced by the high summer temperatures, which led to a temporary cessation in growth. The weekly average water temperatures listed by these authors for the depth of three feet reached 85° F. (29° C.) for one week and remained over 75° F. (24° C.) for sixteen weeks from May 22 to September 18, 1939, with the exception of one week beginning June 12, when the mean temperature was 74° F. (23° C.). A collection made the following week (beginning June 19) exhibited the first accessory mark. Thus age determinations may be unreliable in shallow lakes where very high water temperatures occur over considerable periods.

Spawning

Spawning appears to have little effect on the time of annulus formation. The yellow perch spawn in early spring, but they form their annuli at about the same time as the late spawners. Johnston (1905, 1907), Taylor (1916), Morosov (1924), Hubbs and Cooper (1935), and others record that spawning marks, distinct from true annuli, are formed on scales. Many of the scales examined in this study exhibited accessory checks, which may be interpreted as spawning marks. These structures are most distinct on the anterior field. Further investigation is being carried on in an effort to determine the exact nature of these marks.

Food

Food has been considered of chief importance as a factor in annulus formation by Hoffbauer (1898, 1900), Thomson (1904), Fraser (1917), and Bhatia (1931). Van Oosten (1923), however, stated that

food is only a secondary factor in adults, but may be a primary factor in immature fish.

The author does not believe that food is often the primary factor. It has been shown by several workers (see discussion under "Temperature") that fish eat very little or no food at low temperatures, even when the supply is abundant. It would seem that temperature is more important than food as a factor directly controlling growth.

To be sure, if food is lacking, high temperatures would hardly be expected to induce the resumption of growth, which is essential in annulus formation. According to Hansen (1937), under certain conditions of malnutrition the white crappie (*Pomoxis annularis*), in Illinois, forms an absorption annulus that resembles the spawning mark which develops on the scales of salmon when they are spawning but not feeding. If the absorption of the scale can be taken as an indication of starvation, as Hansen suggested, the late formation of the annulus, found in these fish by Hansen, may well be attributed to a lack of food and a consequently long delay in the resumption of growth. This situation, however, is probably exceptional. The writer did not find any annuli of this absorption type on any of the thousands of scale samples of Michigan fishes.

It is possible also that the metamorphic or "natal" annulus of the Embiotocidae (Hubbs, 1921) is formed on a nutritional basis, for at birth the embryonic food supply is cut off, and retardation or even a temporary stoppage of growth may ensue before the young fish become adapted to the capture of the new type of food.

As Creaser (1926) emphasized, cessation and resumption of growth are the immediate factors involved in the formation of the annulus. Obviously, food can be a primary factor in annulus formation under those conditions in which these changes in growth are primarily determined by the supply of food organisms available.

TIME OF ANNULUS FORMATION

Few references to the time of annulus formation were made by the earlier workers on the age and growth of fishes. For the most part they were content to call the annulus the "winter mark" and apparently gave little consideration to the time of year at which the mark formed. A few men, however, directly or indirectly contributed data on this point.

Johnston (1905) found that the growth had begun at the end of

April on the scales of the salmon (*Salmo salar*) from the River Tay.

For the eel Gemzøe (1908) stated: "The growth of the scales begins in June, or, as a rule, first in July, and is ended at the end of September — sometimes (as in the silver eel) the growth ends somewhat earlier, seldom later."

The year mark was on the edge of the scales of the salmon taken in Ireland during January, February, and March, after which it was found within the edge in an increasing percentage. In May, June, and July collections from Norway the scales had the mark inside the edge in an increasing percentage, although some individual variation occurred (Dahl, 1911).

Lea (1911) showed that many of the herring scales collected on April 5-7 from waters near Bergen, Norway, had a small amount of new growth, whereas others taken at the same time did not. The fish of a sample taken on April 23 had formed new growth on the scales. Concerning Canadian collections, Lea subsequently stated (1919): "These later samples give a more definite idea as to the time when summer growth of the younger herring in these waters [off Prince Edward Island] begins, as in one of the samples (early June) the fish had not commenced their growth, while the remaining samples revealed a distinct new summer belt on the scales.

"An interesting feature in connection with these fish is the fact that summer growth commences so late. Off the coast of Norway, the new summer growth commences in April; but far up in the Baltic, near the coast of Finland, similar conditions are observed. Hellevaara . . ., who has investigated the herring of these waters, observes in this connection: 'Not until the 27th of June did I observe that the scales had begun to grow on the young fish 1 or 2 years old; but not on those which had reached maturity.'"

Sund (1911) found the location of the winter ring to be at the edge of the scales of the sprat (*Clupea sprattus*) taken in April, a short distance inside the margin in those collected in May, and again on the margin in a December sample. (It is doubtful, however, if the new annulus had formed in December).

In River Wye salmon Masterman (1913) discovered a marginal growth band of increasing width from April to September, but not in those taken in November and December.

The year mark is formed on the scales of the squeteague

(*Cynoscion regalis*) and pigfish (*Orthopristis chrysopterus*) in May or June (Taylor, 1916).

Fraser (1917) thus sums up his investigation: "In all scales of salmon [*Oncorhynchus tshawytscha*] caught from January 6 to March 17, there was indication of the check in growth at the margin. On the other hand, with but few exceptions, no scales obtained after April 22, and before November 27, had indication of retardation at the margin. From March 17 to April 22, and from November 27 to January 5, some show retardation at the margin while others do not, this being true even in specimens caught the same day." The author obviously did not distinguish the "dark band" of narrowed circuli from the true annulus. For the chinook salmon of the Columbia and Sacramento rivers Rich (1920) stated that growth is practically negligible from November to March, but more rapid growth is apparently resumed in April and May.

For the herring from the English Channel Hodgson (1925) showed that: "(1). The scales of English herring begin to grow during April and cease to grow in September, irrespective of their geographic position; (2). Younger fish have a longer growing period than older ones; (3). The older fish have a tendency to begin growth later than the younger fish." In Norwegian waters the scales of the herring had begun their growth in May (Lissner, 1925). In the haddock of Scottish waters Thompson (1926) found that the year mark always formed in March.

In 1941 Merriman stated: "Actually for the striped bass, the annulus does not appear in winter, and only becomes evident by April or May."

The papers mentioned above deal chiefly with ocean or river-run fish. Literature dealing with the time of annulus formation in freshwater fishes is also scanty. The following workers, however, have presented some data on the subject.

Van Oosten (1923) states that for the whitefish "the marginal growth is resumed sometime in April (or March?)." Creaser (1926) observed that "At Douglas Lake, Michigan, an investigation of the scales of many of the fishes showed that in June an annulus had only recently been formed."

For the bully (*Gobiomorphus gobiodes*) in the Lower Selwyn River, South Island, New Zealand, Parrott (1934a) wrote: "It should be noticed that the summer annuli [wide circuli] are principally formed

during October, November, and December, while the winter annuli [narrow circuli] are formed principally during March, April, and May. There is, generally speaking, no growth in the scale during June, July, August, and September." He stated, further (1934b), that in the brown trout (*Salmo trutta*) the summer bands begins to develop in September and that by the end of October the majority show summer growth.

On the contrary, Hansen (1937) found that the annuli are formed over a long period in certain waters of Illinois. "In 1935 it was May, June, and July; in 1936, May, June, and possibly July."

According to Eschmeyer (1939), "Annulus formation in some of these immature fish [largemouth bass of Norris Reservoir, Tennessee] therefore extended over a long period, for a few had formed an annulus early in May and others had not begun growth by June 1, assuming that initial growth is reflected on the scale. . . . Two walleyes, taken late in March, had formed no annulus; 21 taken in late May and early June had made some growth; one caught in late May had not yet formed an annulus." In further studies on fish of the Norris Reservoir Jones (1941) determined that the growing season for the smallmouth and largemouth bass begins in June and ends early in October or late in September.

In a study mentioned on page 290 Bennett, Thompson, and Parr (1940) recorded the following observations: "Some of the yearling bluegills had formed annuli on their scales before April 18, and all of them had formed annuli by the end of May. Most breeder bluegills began annulus formation later than the yearlings, and did not complete this formation until October. Annulus formation in the bass extended from mid-April to late September."

For the white perch (*Morone americana*) Cooper (1941) stated that the growing season in Maine in 1940 extended from about the first or the second week in July through August and possibly through part of September.

Hile (1941) discarded a collection of old rock bass captured in Nebish Lake, Wisconsin, on July 5 and 6, 1930, because of his inability to decide whether certain individuals had formed the 1930 annulus. Annulus formation had been completed in the younger rock bass of a collection made July 1 and 2, 1932, in the neighboring Muskellunge Lake, but individuals of the same collection older than six years rarely exhibited a completed year mark.

The time of year at which the annulus forms in Michigan is distinctly earlier in the southern than in the northern part of the state. The extent of the difference is shown in Table II, where it may be seen that the year mark was formed and some marginal growth was evident on the scales of the fishes taken in the southern one third of the Lower Peninsula on May 17-20, 1940, whereas the scales of fish collected in the Upper Peninsula on May 22 had not yet begun to grow.

The statements of the following paragraphs in regard to the time of annulus formation in the different lakes apply to all species in each lake. (For details concerning species and the numbers in the collections see Appendix.) The lakes will be considered in the order in which they appear in Table II, with the exception of Pasinski Pond. The materials from this pond are of such a nature as to require a special discussion.

On some of the scales obtained from Clear Lake (Zone 1) on April 28, 1939, there was an annulus on the edge, and others had a trace of this mark. All those secured on June 1, 1939, when the lake was next fished, exhibited a completed annulus and a margin of new growth. The marginal annulus had formed on some of the scales taken on May 7, 1940, whereas on others there was only a trace or no indication at all of the year mark. The scales next collected here, on June 6, all showed an annulus well inside a margin of growth.

Data pertinent to the problem of the time of formation of the year mark were collected in Deep Lake (Zone 1) in connection with other investigations during 1939, and a special effort was made in 1940 and 1941 to take scale samples at frequent intervals. Certain aspects of these data have been discussed earlier (p. 291), in connection with the study of the factors of annulus formation.

None of the scales had a completed annulus in the first spring collection of April 27, 1939, although a few showed the beginning of one. There was no annulus on the scales taken on April 29. The next collection was made on May 17, at which time an annulus and a narrow band of growth were found on each scale.

In 1940 collections were begun on April 24. Samples taken then and on April 25, 29, 30, May 2, and May 8 had no annulus. On May 10 a few of the scales exhibited an annulus. On May 13-14 all but six of the samples had the year mark at the margin. Collections of May 20-22 showed the annulus within a narrow but distinct margin of growth.

TABLE II
TIME OF ANNULUS FORMATION ON THE SCALES OF GAME FISHES IN MICHIGAN
(See Appendix for details concerning the collections on which this table was based.)

Year	Zone	Lake	Dates when no scales had formed a marginal annulus		Dates when some scales had formed a marginal annulus			Dates when all scales had formed a marginal annulus	
			Date	Number of specimens	Date	Number of specimens		Date	Number of specimens
1939	1	Clear	Jan. 19	2	April 28	with	without	June 1	59
			Feb. 25, 28	15	...	7	6	July 15	32
		Pasinski Pond	April 18	46	...	...	...	Dec. 31	14
			April 23	152	...	...	...	April 29	38
			...	...	...	...	...	May 28	69
	2	Deep	Feb. 2	2	...	...	...	June 14-Oct. 12	327
			April 27	8	...	...	...	May 17	38
		April 29	5	...	...	...	May 19-31	56	
		...	...	May 17	59	14	June 2-Aug. 4	169	
		...	...	...	...	...	June 19	175	
3	Round	...	...	...	...	...	Oct. 28	17	
		...	...	...	...	...	May 25	15	
	North Manis- tique	...	...	...	...	...	June 24	77	
		...	...	...	...	...	Oct. 20	7	
		...	...	...	...	...	June 26	76	
...	...	...	...	...	July 28	111			
...	...	...	...	...	Sept. 7	21			
...	...	...	...	...	Oct. 21	15			

The 1941 collections were begun on April 22, on which date only one bluegill revealed a marginal annulus. On April 24, 26, and 28, and May 1 and 3 increasing percentages of the scales had a marginal annulus. After May 3 all samples bore a marginal annulus with some growth beyond the annulus.

The annulus was just inside the edge on the majority of the scales of fish taken from Budd Lake (Zone 2), May 17-18, 1939, but only a few of those caught on May 17, 1940, had an annulus. All scales collected on June 19, 1939 and 1940, showed an annulus with a marginal growth.

On the scales secured in Round Lake (Zone 2) on May 26-28, 1939, the annulus was just inside the margin. In the next collection, made on June 21-23, an annulus was present within a wide band of growth on all fish. In 1940, scales collected on May 20 had no annulus, but all of those taken on June 19 exhibited an annulus inside the scale margin.

The annulus was on the edge of some scales collected in North Manistique Lake (Zone 3) on June 25, 1939, and a few scales had a slight marginal growth. In 1940 a collection made here on May 22 gave no indication that an annulus had been laid down. On June 24, when the next sample was obtained, the annulus had been formed on all specimens, with a slight marginal growth on some.

In Bass Lake (Zone 3) the annulus was obvious on all specimens when a collection was made on June 25, 1939. All scales taken on July 28-29 showed a band of marginal growth that was distinctly wider than that on the scales of the previous collection. In 1940 a sample was taken on May 24, at which time no annulus was apparent. When the next collection was made, on June 25, the annulus had formed on all scales.

Collections were made on July 1-3, 1939, in Crooked Lake (Zone 3). The annulus was to be seen on the edge of the scales. In 1940 a collection made in May showed no annulus present. All scales collected on June 26, 1940, had an annulus near the edge.

On the scale samples secured from Lake Fannie Hooe (Zone 3) on July 4-6, 1939, the annulus was just inside the edge of all except a few, which had a fair amount of marginal growth. No annulus was present on any of the scales collected on May 27-28, 1940. The next collection, taken on June 27-28, showed an annulus near the edge of all scales.

Additional scattered material was obtained through samples of scales taken in the springs of 1939 and 1940 from other lakes that were visited during the investigation of other problems. Others were obtained from Standard Lake (Zone 2) during May and June, 1939, and from Ford Lake (Zone 2) in May, 1939, and May, 1940. Samples were kept from fish caught in June, 1940, during a survey of certain lakes in Menominee County (Zone 3). In all these samples the indicated time of annulus formation agreed with the findings for the selected lakes in the same region.

The data on the bluegills of Pasinski Pond not only provide information concerning the time of annulus formation but also yield strong evidence in support of the belief that only one annulus is formed each year. The annulus formed on the scales of bluegills (the only game fish present) in the pond (Zone 1) between April 23 and 29, 1939. None of the scales collected on April 23 had a marginal annulus, but the year mark was evident on the scales of all fish taken on April 29. It was impossible to continue the observations here beyond the growing season of 1939 because this pond suffered a complete winterkill in February, 1940. This event was particularly unfortunate since the fish were of known age and many had been jaw-tagged.

The second-year growth of these fish (all known to be yearlings) up to different times of capture in the growing season is described as the percentages of the average "expected" growth for the entire growing season of 1939. This average full-season growth, derived from the measurements of the scales of 164 bluegills taken at the time of the winterkill is indicated by the heavy vertical line on the graph (Fig. 2). The range of length and the number of specimens on which each percentage is based are shown by the frequency curves. The mean growth of each collection is represented by a broken vertical line.

It will be seen that on April 23 no fish had an annulus, but an annulus with a small amount of marginal growth was present in all specimens in the collection of April 29. A steady increase in the percentage of the annual growth completed occurred in the succeeding collections. Though the range of variation increased somewhat during the season, none of the fish taken in May, June, or July had the annulus sufficiently close to the margin to indicate recent formation. By July approximately 85 per cent of the "expected" growth for

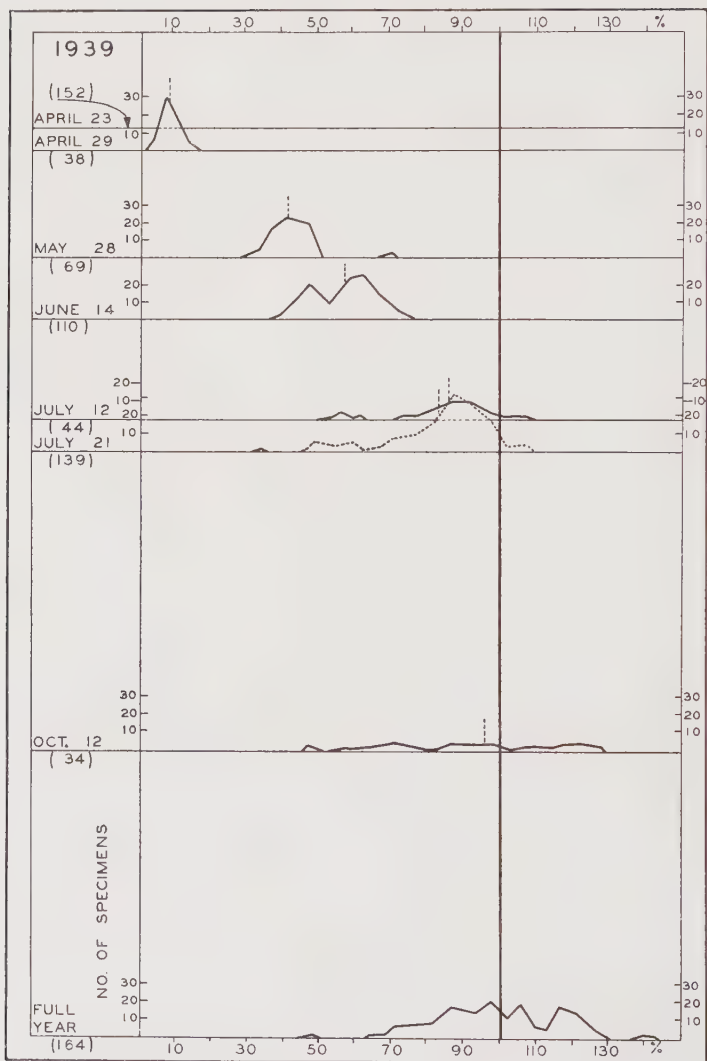


FIG. 2. Percentage of "expected" annual scale growth completed on different dates by yearling bluegills from Pasinski Pond in 1939. Number of specimens in parentheses. Heavy solid line indicates the mean of the full year's growth. Broken lines indicate the means of the individual collections

the season had been completed. In October a small collection showed that 96 per cent of the "expected" growth had been attained. When the fish were killed in February, 1940, they had not yet formed the second annulus, but undoubtedly would have completed this structure in the spring had they lived.

The relatively small variation in the amount of the marginal growth on the scales of the Pasinski Pond bluegills caught on the same date and the increase of this growth during the summer are illustrated by the photographs in Plates II-IV. The scales that are pictured were taken at random from the collections of the dates listed.

The data for other waters as well as for Pasinski Pond indicate uniformly that only one annulus is formed each year. For a number of species and in several lakes the relative amounts of the annual scale growth outside the marginal annulus were calculated for each date of sampling. Table III shows the typical results of the calculations. The amount of growth at any date is given as the percentage of the "expected" full-season growth for fish in that particular year of life. The "expected" annual scale growth was determined as the mean of the full-season increments of the scale for each year of life for all specimens that had survived beyond that year. For example, the average scale growth for the first year of life was based on the growth made in that year by all fish in the collection one year old and older, and that for the second year was based on all fish two years old and older, and so on. The percentage of scale growth completed at the time of capture was obtained by dividing the average growth outside the annulus by the average full-season growth expected for fish in the same year of life. The table shows that the annulus formed between certain dates and that in successive collections lay farther and farther within the scale margin. It may be seen also from Table III that in Deep Lake, as in Pasinski Pond, all annuli were completed within a very short period. It is believed that the annulus forms rapidly in all lakes.

The time of annulus formation is correlated roughly with the mean monthly air temperatures. At comparable dates the springs of 1939 and 1941 were warmer than the spring of 1940, and the annulus formed earlier in 1939 and 1941 than in 1940. Since water temperature and air temperature are correlated rather closely, it is to be expected that the water would become warmer earlier in a warm

TABLE III

SCALE GROWTH OUTSIDE MARGINAL ANNULUS, AS THE PERCENTAGE OF THE EXPECTED TOTAL GROWTH FOR THE GIVEN YEAR

The average expected scale growth for a particular year of life was based on average measurements of the scale growth of all fish that had completed that year of life. The data are based on collections from Deep Lake.

Species and date	Age group						
	I	II	III	IV	V	VI	VII
Bluegill							
February 4, 1939	...	...	...	...	0 (2)	...	...
April 27, 29	...	...	...	0 (2)	0 (5)	...	...
May 17, 19, 21, 27	...	...	17 (10)	20 (25)	33 (14)	44 (1)	...
June 5, 8, 13, 20, 28	...	25 (1)	35 (17)	38 (27)	40 (9)	...	...
July 2, 5, 7, 13, 24, 26 ..	44 (2)	47 (15)	57 (10)	51 (17)	61 (3)	...	...
August 2, 4	...	78 (1)	78 (3)	64 (6)	...	...	...
April 29, 1940	...	...	0 (1)	...	...	...	...
May 2, 8	...	...	0 (4)	0 (3)	...	...	...
May 10	...	0 (2)	*0.8 (6)	0 (2)	...	...	...
May 13, 14	...	...	5 (11)	7 (5)	13 (7)	12 (6)	0 (1)
May 20, 22, 27	...	...	...	15 (5)	24 (5)	35 (3)	...
June 14	115 (2)	37 (5)	30 (12)	32 (2)	44 (1)	...	...
Pumpkinseed							
April 27, 1939	...	...	...	...	0 (1)	...	...
May 17, 21, 27	...	...	...	...	27 (20)	...	...
June 5, 8, 13, 20, 28	...	...	...	...	53 (7)	...	...
July 2, 12, 13, 24	62 (3)	51 (10)	50 (2)	62 (5)	103 (2)	...	...
August 2	...	...	...	...	77 (2)	...	...
April 25, 29, 30, 1940	...	...	0 (7)	0 (5)	0 (4)	0 (4)	...
May 2, 8	...	...	0 (6)	0 (4)	0 (9)	0 (4)	0 (1)
May 10	...	...	*1 (2)	*3 (2)	...	...	0 (1)
May 13, 14	...	...	*10 (7)	13 (5)	4 (1)	...	...
May 20, 22, 27	...	...	27 (2)	34 (4)	36 (3)	...	...
June 14	...	38 (2)	49 (15)	54 (1)	...	...	...

* Some with or without growth

spring than in a cold one. When the lakes of the southern part of the Lower Peninsula have become sufficiently warm to permit the resumption of fish growth, the lakes in the Upper Peninsula are barely ice-free. As the temperatures gradually increase in the north, growth of the fish in these lakes is finally resumed, with the resultant annulus formation. Since the local temperature conditions vary

considerably from year to year, and since the isotherms form irregular patterns, it was found impracticable to delimit on the basis of isotherms the zones or sections which are needed for a further analysis of the variations throughout the state in the time of annulus formation. The lines of separation of three general areas or zones were set somewhat arbitrarily as Town Line 10 North and the Straits of Mackinac. Zone 1 extends from the southern boundary of the state north to Town Line 10; Zone 2 covers the Lower Peninsula north of this line; and Zone 3 comprises the entire Upper Peninsula (Fig. 1). It must be remembered that the temperatures decrease gradually toward the north, and it has been found that the time of annulus formation shows a similar gradient, without the abrupt discontinuities that zones are likely to suggest.

It is estimated that in an "average" year the annulus is usually completed in Zone 1, the southern one third of the Lower Peninsula, by the middle of May; in Zone 2, the northern two thirds of the Lower Peninsula, by the first part of June; and in Zone 3, the Upper Peninsula, by the end of June. The date of actual completion will vary somewhat according to temperature conditions in different localities and in different years.

SUMMARY

1. The investigation of annulus formation on the scales of some of the game fishes of Michigan was begun in 1939 under the sponsorship of the Michigan Institute for Fisheries Research.

2. Scale samples were collected at regular intervals from seven lakes and a pond; additional samples were taken from other lakes in connection with other investigations.

3. Temperature appears to be the primary factor in annulus formation.

4. Spawning was found to have little or no effect on the time of annulus formation.

5. Food is ordinarily of secondary importance as a factor in the time of annulus formation. A severe scarcity of food, or an abrupt change in the availability of food, may make it a primary factor.

6. The mean temperatures of the days on which the scales in the collections first showed annuli were 53° F. in 1940 and 52° F. in 1941. The mean temperatures of the first days on which the majority of the scale samples showed an annulus were 58° F. in both 1940 and 1941.

7. The annulus formed earlier in 1939 and 1941 than in 1940. The earlier formation in 1939 and 1941 was correlated with the higher temperatures at corresponding dates in those two years.

8. The time of annulus formation was progressively later from the southern part of Michigan to the northern part.

9. The state was divided arbitrarily into three zones: Zone 1, roughly the southern one third of the Lower Peninsula; Zone 2, the northern two thirds of the Lower Peninsula; and Zone 3, the Upper Peninsula. In all but exceptionally cold years the formation of the annulus may be expected to be completed in Zone 1 by the middle of May; in Zone 2, by the first part of June; and in Zone 3, by the end of June. Annual fluctuations in temperature may bring about some variation in the date of formation of the year mark.

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APPENDIX

DETAILED DATA ON THE TIME OF ANNULUS FORMATION ON THE SCALES OF MICHIGAN GAME FISHES

The data of Table III on the time of annulus formation on the scales of Michigan game fishes are not presented by species. The following data show definitely that the different species formed the year mark simultaneously as they started to grow in the spring.

CLEAR LAKE, JACKSON COUNTY

Data for 1939

Annulus not yet formed at the margin:

January 19: 2 black crappies

February 25, 28: 15 bluegills

Marginal annulus formed in some specimens:

April 28: 6 perch with annuli, 2 without; 2 bluegills without; 1 rock bass without; 1 black crappie with, 1 without

Annulus formed on all scales:

June 1: 12 perch, 6 largemouth bass, 19 bluegills, 2 rock bass, 16 pumpkin-seeds, 4 black crappies

July 15: 6 perch, 5 largemouth bass, 13 bluegills, 8 pumpkinseeds

December 31: 6 bluegills, 8 black crappies

Data for 1940

Marginal annulus formed in some specimens:

May 7: 3 largemouth bass without annuli; 2 bluegills with, 22 without; 10 pumpkinseeds with, 4 without; 1 green sunfish $\times$ bluegill with, 2 without

Annulus formed on all scales:

June 6: 17 perch, 6 largemouth bass, 9 bluegills, 9 rock bass, 6 pumpkinseeds, 4 black crappies, 2 green sunfish

BUDD LAKE, CLARE COUNTY

Data for 1939

Marginal annulus formed in some specimens:

May 17: 21 perch with annuli, 9 without; 24 bluegills with; 5 pumpkinseeds with, 4 without; 3 largemouth bass with, 1 without; 2 rock bass with; 1 black crappie with; 3 pumpkinseed $\times$ green sunfish with

Annulus formed on all scales:

June 19: 52 perch, 29 bluegills, 70 pumpkinseeds, 13 largemouth bass, 1 green sunfish, 4 rock bass, 3 black crappies, 2 bluegill $\times$ pumpkinseed, 1 pumpkinseed $\times$ green sunfish

October 28: 1 perch, 3 bluegills, 6 pumpkinseeds, 2 largemouth bass, 5 rock bass

Data for 1940

Marginal annulus formed in some specimens:

May 17: 7 perch with annuli, 20 without; 1 bluegill with, 31 without; 3 pumpkinseeds with, 5 without; 6 largemouth bass without; 1 green sunfish without; 9 rock bass with, 10 without; 2 black crappies without; 5 pumpkinseed $\times$ green sunfish without

Annulus formed on all scales:

June 19: 14 perch, 16 bluegills, 15 pumpkinseeds, 8 largemouth bass, 1 green sunfish, 3 rock bass

ROUND LAKE, EMMET COUNTY

Data for 1939

Annulus formed on all scales:

May 25: 10 pumpkinseeds, 5 rock bass

June 24: 25 pumpkinseeds, 19 bluegills, 21 perch, 12 rock bass

October 20: 1 pumpkinseed, 3 bluegills, 2 rock bass, 1 largemouth bass

Data for 1940

Annulus not yet formed at margin:

May 20: 6 pumpkinseeds, 4 rock bass, 3 largemouth bass

Annulus formed on all scales:

June 21: 22 pumpkinseeds, 18 bluegills, 2 perch, 7 rock bass, 1 largemouth bass

NORTH MANISTIQUE LAKE, LUCE COUNTY

Data for 1939

Annulus formed on all scales:

June 26: 32 rock bass, 27 perch, 9 walleyes, 8 smallmouth bass

July 28: 43 rock bass, 61 perch, 6 walleyes, 1 smallmouth bass

September 7: 5 rock bass, 8 perch, 8 walleyes

October 21: 2 rock bass, 7 perch, 6 walleyes

Data for 1940

Annulus not yet formed at margin:

May 23: 28 rock bass, 18 perch, 7 walleyes

Annulus formed on all scales:

June 24: 8 rock bass, 16 perch, 4 walleyes

July 21: 16 rock bass, 21 perch, 6 walleyes, 6 smallmouth bass

BASS LAKE, MARQUETTE COUNTY

Data for 1939

Annulus formed on all scales:

June 25: 14 pumpkinseeds, 2 pumpkinseed $\times$ bluegill

July 4: 8 bluegills, 16 pumpkinseeds, 1 perch

July 29: 41 bluegills, 19 pumpkinseeds, 6 perch, 3 walleyes, 3 largemouth bass

September 15: 3 bluegills, 1 pumpkinseed, 2 walleyes

October 22: 8 bluegills, 6 perch, 1 largemouth bass, 1 smallmouth bass

Data for 1940

Annulus not yet formed at margin:

May 24: 17 bluegills, 10 pumpkinseeds, 4 perch, 1 walleye, 3 largemouth bass,
1 smallmouth bass

Annulus formed on all scales:

June 25: 10 bluegills, 7 pumpkinseeds, 5 perch, 6 walleyes, 1 largemouth bass

July 24: 30 bluegills, 7 pumpkinseeds, 18 perch, 2 walleyes, 1 largemouth
bass, 1 smallmouth bass

CROOKED LAKE, GOGEBIC COUNTY

Data for 1939

Annulus formed on all scales:

July 3: 32 perch, 11 bluegills, 9 smallmouth bass, 5 largemouth bass, 2 black
crappies, 9 pumpkinseeds

July 31: 16 perch, 4 bluegills, 9 smallmouth bass, 6 largemouth bass, 1 black
crappie, 2 pumpkinseeds

August 26: 54 perch, 8 bluegills, 1 smallmouth bass, 6 largemouth bass, 1 black
crappie

October 23: 9 perch, 2 bluegills, 2 smallmouth bass, 1 pumpkinseed

Data for 1940

Annulus not yet formed at margin:

May 26: 22 perch, 1 bluegill, 1 smallmouth bass, 6 black crappies

Annulus formed on all scales:

June 27: 15 perch, 2 bluegills

July 27: 38 perch, 6 bluegills, 3 largemouth bass, 2 black crappies

LAKE FANNIE HOOE, KEWEENAW COUNTY

Data for 1939

Annulus formed on all scales:

July 4-6: 19 rock bass, 8 perch, 3 smallmouth bass, 1 bluegill

August 2-4: 21 rock bass, 27 perch

August 30: 4 rock bass, 7 perch

October 24: 1 rock bass, 1 perch

Data for 1940

Annulus not yet formed at margin:

May 27-28: 4 rock bass, 7 perch, 1 bluegill

Annulus formed on all scales:

June 27: 10 rock bass, 8 perch

July 27-29: 19 rock bass, 20 perch

DEEP LAKE, OAKLAND COUNTY

Data for 1939

Annulus not yet formed on margin:

February 2: 2 bluegills

April 27: 5 rock bass, 1 pumpkinseed, 2 bluegills

April 29: 5 bluegills

Annulus formed on all scales:

May 17: 14 rock bass, 15 pumpkinseeds, 9 bluegills

May 19: 1 pumpkinseed, 2 bluegills

May 21: 1 rock bass, 1 pumpkinseed, 20 bluegills

May, June, July, August: 10 rock bass, 46 pumpkinseeds, 144 bluegills

Data for 1940

Annulus not yet formed at margin:

April 24: 1 rock bass

April 25: 1 pumpkinseed

April 29: 7 rock bass, 4 pumpkinseeds, 1 bluegill

April 30: 2 rock bass, 15 pumpkinseeds, 2 largemouth bass

May 2: 5 rock bass, 16 pumpkinseeds, 3 bluegills, 2 largemouth bass

May 8: 16 rock bass, 7 pumpkinseeds, 4 bluegills

Marginal annulus formed in some specimens:

May 10: 2 rock bass with annuli, 14 without; 2 pumpkinseeds with, 11 without; 1 bluegill with, 9 without; 1 largemouth bass without

May 13: 7 rock bass with annuli, 1 without; 8 pumpkinseeds with, 22 bluegills with, 2 without

- May 14: 7 rock bass with annuli, 1 without; 7 pumpkinseeds with, 1 without;
 7 bluegills with, 1 without
 Annulus formed on all scales:
 May 20: 4 rock bass, 2 pumpkinseeds, 5 bluegills •
 May 22: 1 rock bass, 4 pumpkinseeds, 9 bluegills
 May 27: 1 rock bass, 4 pumpkinseeds, 2 bluegills, 2 largemouth bass
 June 14: 5 rock bass, 18 pumpkinseeds, 22 bluegills

Data for 1941

Marginal annulus formed in some specimens:

- April 22: 2 pumpkinseeds without annuli; 1 bluegill with, 16 without
 April 24: 2 rock bass with annuli, 8 without; 6 pumpkinseeds with, 17 without; 4 bluegills with, 14 without
 April 26: 5 pumpkinseeds with annuli, 9 without; 8 bluegills with, 16 without
 April 28: 5 rock bass with annuli; 8 pumpkinseeds with, 5 without; 12 bluegills with, 4 without
 May 1: 3 rock bass with annuli; 11 pumpkinseeds with, 2 without; 6 bluegills with, 1 without
 May 3: 4 rock bass with annuli; 11 pumpkinseeds with; 9 bluegills with, 1 without

Annulus formed on all scales:

- May 5: 2 rock bass, 5 pumpkinseeds, 3 bluegills
 May 7: 2 rock bass, 4 pumpkinseeds, 2 bluegills
 May 9: 1 rock bass, 2 bluegills
 May 12: 2 rock bass, 4 pumpkinseeds, 2 bluegills
 May 16-24: 7 rock bass, 17 pumpkinseeds, 23 bluegills

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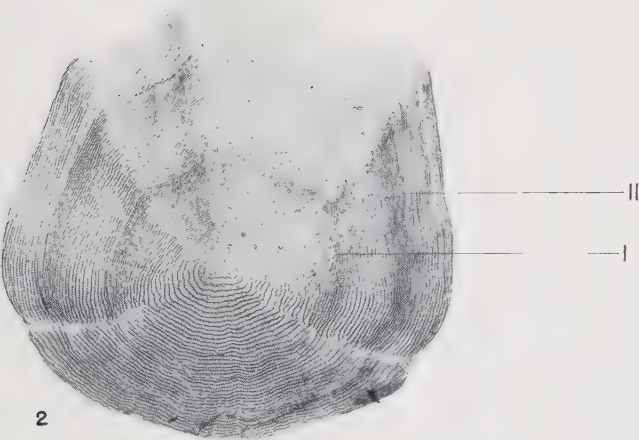
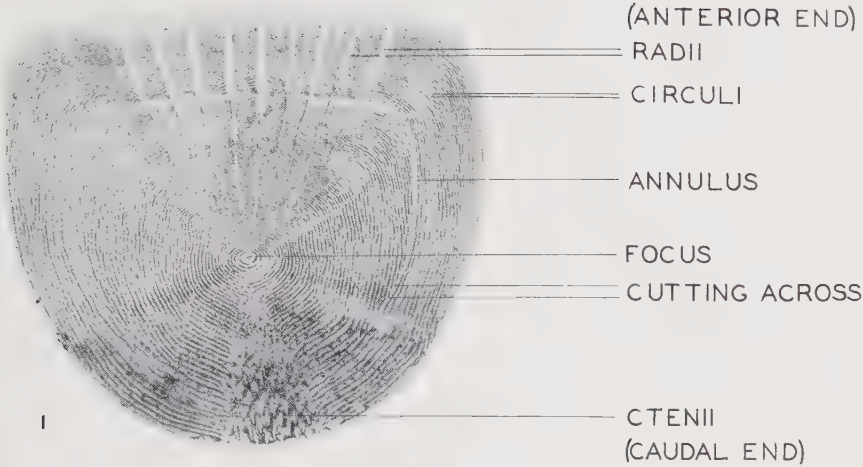


FIG. 1. Ctenoid scale from a bluegill $4\frac{1}{4}$ inches long. Age one year

FIG. 2. Cycloid scale from a cisco 11 inches long. Age two years

(Annuli indicated by Roman numerals)



Scales of bluegills (size range, $2\frac{7}{8}$ - $4\frac{1}{4}$ inches, total length) taken from Pasinski Pond, Livingston County, Michigan, April 23, 1939. No annulus present.

(All photographs in Plates II-IV taken at a magnification of 44.3)



Scales of bluegills (size range, $2\frac{3}{4}$ – $4\frac{1}{4}$ inches, total length) taken from Pasinski Pond
April 29, 1939. Annulus at edge



Scales of bluegills (size range, $2\frac{3}{4}$ – $4\frac{1}{4}$ inches, total length) taken from Pasinski Pond, June 14, 1939. Annulus well inside margin of growth

